

**NATURAL ENEMIES OF THE CRYPTIC AND SYMPATRIC SPECIES,  
*TRUPANEA NIGRICORNIS* (COQUILLET), A POLYPHAGE, AND THE  
NARROWLY OLIGOPHAGOUS *T. BISETOSA* (COQUILLET)  
(DIPTERA: TEPHRITIDAE)**

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*Abstract.*—The flower head-infesting tephritids *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett) occur in sympatry in southern California. They are closely related cryptic species and difficult to differentiate morphologically. However, *T. nigricornis* behaves as a generalist infesting at least eight tribes of the Asteraceae while *T. bisetosa* is mainly a specialist on wild sunflowers. This study investigates the types of natural enemies that attack *T. nigricornis* and *T. bisetosa* and whether the difference in diversity and densities of parasitoids attacking the two cryptic species help to explain their different modes of herbivory. Results showed that percentage parasitism was much higher in samples infested with *T. nigricornis* (21.5–58.2%) than *T. bisetosa* (4.5–16.1%). The generalist species was also attacked by more species of parasitoids than the specialist species (5 vs. 1). Moreover, there were fewer samples yielding *T. nigricornis* that were free of parasitoids than samples yielding *T. bisetosa* free of parasitoids. Therefore, by overcoming the tough biophysical features of wild sunflowers such as resins and hard bracts, host specialization by *T. bisetosa* may provide escape from natural enemies.

*Key Words:* Natural enemies, Tephritidae, *Trupanea*, parasitoids, sympatry, cryptic species, enemy-free space, polyphagy, oligophagy

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The flower head-infesting tephritids *Trupanea nigricornis* (Coquillett) and *T. bisetosa* (Coquillett) are closely related species that occur in sympatry in southern California (Foote et al. 1993). They are considered cryptic species as all immature stages are highly similar and difficult to separate (Knio et al. 1996a), and the adults show great morphological similarities (Cavender and Goeden 1983). However, the two species can be differentiated behaviorally and ecologically. *Trupanea nigricornis* is a generalist,

attacking the flower heads of at least 71 species of Asteraceae belonging to 8 tribes and 33 genera. On the other hand, *T. bisetosa* is an oligophagous species so far known to attack only 6 species of Asteraceae belonging to only one tribe, the Heliantheae (Goeden 1985, 1992). Subtle differences were detected in the courtship and mating behaviors of the two species, but the main behavioral distinction was in the oviposition behavior of the females. *Trupanea nigricornis* females pierced the plant's host tissues

during oviposition in a way that the posterior ends of the eggs were always inserted in the immature achene or corolla's tissues while *T. bisetosa* females deposited their eggs loosely among the corolla tubes without injuring the host tissues. The oviposition behavior of *T. bisetosa* females was critical to their survival and is an adaptation to their most common host, wild sunflowers, *Helianthus annuus* L., that exude sticky resins when injured, fatally entrapping females that accidentally puncture plant tissues during oviposition (Knio et al. 1996b).

Resource utilization studies showed that the larvae of *T. nigricornis* and *T. bisetosa* exploited the flower heads of their hosts in a similar way and the percentage of damaged achenes per larva was similar in both species, taking into account the flower head size (Knio et al. 2001). However, the fecundity of *T. nigricornis* was higher and the percentage of flower heads infested by *T. nigricornis* in the field was higher than the percentage of flower heads infested by *T. bisetosa*. Moreover, the number of collected samples of *T. nigricornis* hosts that did not yield any *T. nigricornis* was much lower than the number of *T. bisetosa* hosts not yielding any *T. bisetosa* (Knio et al. 2001).

One factor that molds the community structure of phytophagous insects is interspecific competition. In many cases, interspecific competition is low because the population densities of phytophagous insects are kept at low levels as a result of predation and parasitism (Strong et al. 1984). In previous studies by Knio et al. (2001), it was shown that *Trupanea nigricornis* and *T. bisetosa* follow several evasion strategies that reduce interspecific competition. However, the impact of natural enemies on population densities of both species was not evaluated. This study focuses on the diversity and density of parasitoids

attacking *T. nigricornis* and *T. bisetosa* natural populations. It is one of a series of comparative studies intended to shed light on the nature of polyphagy/oligophagy in the closely related, sympatric, cryptic species, *T. nigricornis* and *T. bisetosa*.

#### MATERIALS AND METHODS

Parasitism of the immature stages of *T. nigricornis* and *T. bisetosa* was studied by examining field-collected flower heads of Asteraceae in the laboratory. Flower head samples of the host plants of *T. nigricornis* and *T. bisetosa* were collected during four years from 42 interior valley and desert sites in southern California. The host plants of *T. nigricornis* included *Encelia farinosa* Gray, *E. frutescens* Gray, *E. virginensis* A. Nelson, *Haploppappus acradenius* (Greene) Hall, *H. venetus* (Humboldt) Blake, and *Viguiera deltoidea* Gray. Sampled host plants of *T. bisetosa* were *Helianthus annuus* L., *H. niveus* (Bentham) Brandegee, and *Geraea canescens* A. Gray.

Every sample consisted of mature flower heads (100–1,500) picked at random from different plants at each site, stored in a plastic bag, and transported in an ice chest to the laboratory. All samples were stored under refrigeration until processed.

For every sample, flower heads were counted, then dissected and examined in the laboratory under a stereomicroscope until obtaining a subsample of 25 infested flower heads. The following data were recorded: number, size (length and diameter) and stage of *T. nigricornis*/*T. bisetosa* larvae and puparia; state of the larvae (healthy, feeding, discolored, sluggish, parasitized, dead); presence of external parasites feeding on the larvae; number and stages of other insect species.

Third instars and puparia removed from the dissected flower heads were placed individually in small glass vials

plugged with cotton to capture the emerging insect (adult fly or parasite) and determine the number of days from caging to emergence. These vials were held in a humidity chamber (76%) in the laboratory and checked daily for emergence.

The remaining flower heads in every sample were placed in glass-topped, sleeve, cages (34×32×35 cm) in the insectary at the University of California, Riverside at 60% RH and 12/12 (LD) photoperiod from 0500–1700 h. The numbers and identities of the insects and parasitoids that emerged were recorded.

Percentage parasitism in samples was estimated by dividing the number of parasitoids emerged by the total number of dipterous insects and parasitoids obtained from that sample, including reared dipterous insects from the dissected subsample. Only species confirmed as parasitoids of *T. nigricornis* and *T. bisetosa* from individually reared host larvae or puparia were included in the calculation of percentage parasitism; however, we assumed that these parasitoids did not distinguish among dipterous larvae as some of the species were reared from other dipterous insects, e.g., Agromyzidae associated with *T. nigricornis* and *T. bisetosa* flower heads. Percentage parasitism was only calculated from samples that yielded tephritids and parasitoids; the samples that yielded tephritids, but no parasitoids, were listed separately.

The parasitoids were identified by J. LaSalle. Voucher specimens of *T. nigricornis*, *T. bisetosa* and their parasitoids are housed in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM).

#### RESULTS AND DISCUSSION

The data obtained from dissecting samples of flower heads collected over a four year period showed that the

immature stages of *T. nigricornis* suffered mortality due to parasitism by several species of Pteromalidae and other chalcidoid Hymenoptera, while those of *T. bisetosa* suffered mortality due to parasitism by only one species of Pteromalidae (Table 1). Rearing records of individual larvae and puparia confirmed the following five species as parasitoids of *T. nigricornis*: *Halticoptera* sp. (Pteromalidae), *Pteromalus* sp. 1 (Pteromalidae), *Colotrechnus ignothus* Burks (Pteromalidae), *Eurytoma* sp. (Eurytomidae), and an unidentified perilampid (Perilampidae). Rearing of individual puparia of *T. bisetosa* confirmed *Pteromalus* sp. 2 (Pteromalidae) as the sole parasitoid of *T. bisetosa* (Table 1). The *Pteromalus* specimens from *T. nigricornis* and *T. bisetosa* were determined only to genus; although they are superficially similar, further work should be conducted to determine if they are different species or not. We have labeled them 1 and 2 to clarify associations only.

The two pteromalids, *Halticoptera* sp. (subfamily Miscogasterinae) and *Pteromalus* sp.1 (subfamily Pteromalinae) were identified as primary, solitary, internal larval-pupal parasitoids of *T. nigricornis*. Neither parasitoid species altered the shape of the larva or puparium during feeding. Parasitized *T. nigricornis* larvae continued to feed and grow. Adult parasitoids later emerged from their host puparia. The presence of the parasitoid was not suspected until its emergence. The size of the puparia from which either *Halticoptera* sp. or *Pteromalus* sp. emerged fell within the normal size range (1–1.25 mm in diameter, and 2.5–3 mm in length) of *T. nigricornis* puparia as reported by Knio et al. (2001). The behavior of the parasitized larvae also was not altered. Parasitized third instar larvae (n = 5) removed from dissected flower heads and individually reared pupated like healthy larvae of *T. nigricornis*. The length of time from



Table 1. Rearing records of the parasitoids isolated from individual puparia of *Trupanea nigricornis* and *T. bisetosa* dissected from flower heads of different hosts.

Host Plant	N <sup>a</sup>	Parasitoid Species	Number Reared Females: Males		Number of Days to Emergence <sup>b</sup>
<i>T. nigricornis</i> hosts:					
<i>E. farinosa</i>	12	<i>Halticoptera</i> sp.	13	11	4–25
	3	<i>Pteromalus</i> sp. 1	6	1	14
	1	Perilampid	1	—	56
<i>E. frutescens</i>	8	<i>Halticoptera</i> sp.	8	1	7–25
	4	<i>Pteromalus</i> sp. 1	5	3	6–20
	1	<i>Eurytoma</i> sp.	1	—	106
	1	Perilampid	1	1	81–111
<i>E. virginensis</i>	3	<i>Halticoptera</i> sp.	3	1	9–10
	3	<i>Pteromalus</i> sp. 1	4	1	7–10
	4	<i>Colotrechnus ignothus</i>	4	4	12–13
	1	<i>Eurytoma</i> sp.	1	1	—
<i>H. acradenius</i>	1	<i>Pteromalus</i> sp. 1	1	1	10
	1	<i>Eurytoma</i> sp.	—	1	24
<i>T. bisetosa</i> hosts:					
<i>H. annuus</i>	3	<i>Pteromalus</i> sp. 2	4	4	10–12

<sup>a</sup> Number of sites where flower head samples were collected and that yielded the specific parasitoid species.

<sup>b</sup> Number of days from the time third instar larvae or puparia were dissected out of the flower heads and individually caged until the emergence of the parasitoids.

caging to emergence of the parasitoids was similar to that observed for *T. nigricornis* adults: ca. 13 days ( $12.83 \pm 2.02$  (SE); range: 4–25;  $n = 12$ ) for *Halticoptera* sp. and ca. 12 days ( $11.88 \pm 1.7$ ; range: 6–20;  $n = 8$ ) for *Pteromalus* sp. (Table 1).

Both of these parasitoids were also recovered from other insects associated with *T. nigricornis* host plants. *Halticoptera* sp. was reared from individual puparia of *Melanagromyza viridis* (Frost) (Agromyzidae), but not from *Neotephritis finalis* Loew (Tephritidae), a common insect infesting *Encelia* species. *Pteromalus* sp. was reared from individual puparia of both *M. viridis* and *N. finalis*. Goeden et al. (1987) also identified *Pteromalus* sp. as a larval-pupal parasitoid of *N. finalis*.

*Halticoptera* and *Pteromalus* spp. seem to be common parasitoids of flower head-infesting tephritids. *Pteromalus purpureiventris* (Ashmead) was reported as a primary, solitary larval-pupal parasitoid of *T. conjuncta* (Adams) (Goeden

1987) and *T. imperfecta* (Coquillett) (Goeden 1988). *Pteromalus coloradensis* (Ashmead) was identified as a larval-pupal parasitoid of *Paracantha gentilis* Hering, and it was the only parasitoid recovered from this tephritid (Headrick and Goeden 1989). Unidentified *Pteromalus* spp. were reared as primary, solitary parasitoids of *Tomoplagia cressoni* Aczél (Goeden and Headrick 1991a), *Procecidochares lisae* Goeden (Silverman and Goeden 1980; as *Procecidochares* sp.), and *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1984). *Halticoptera stella* Girault was reared from galls of *Procecidochares lisae* (Silverman and Goeden 1980). Both *Halticoptera* sp. and *Pteromalus* sp. were reported as parasitoids of *Tephritis baccharis* (Coquillett) (Goeden and Headrick 1991b). However, unlike the larval-pupal *Halticoptera* sp. parasitizing *T. nigricornis*, the *Halticoptera* sp. parasitizing *T. baccharis* was an external larval parasitoid (Goeden and Headrick 1991b).

*Pteromalus* sp. 2 was also the only parasitoid reared from individual puparia of *T. bisetosa*. As with *T. nigricornis*, *Pteromalus* sp. 2 was identified as a solitary, primary, larval-pupal parasitoid of *T. bisetosa*. The number of days from caging to emergence was 10–12 days ( $11 \pm 1$ ;  $n = 2$ ) (Table 1). Similarly, Cavender and Goeden (1982) recovered *Pteromalus* sp. (as *Habrocytus* sp.) from *T. bisetosa* puparia, and also reared *Bracon nuperus* Cresson from *T. bisetosa* larvae. In this study, three external hymenopterous parasitoid larvae were observed to feed on *T. bisetosa* larvae, but were not successfully reared to adulthood.

A third pteromalid parasitoid of *T. nigricornis* was *Colotrechnus ignothus*, which was identified as an external larval parasitoid. *Colotrechnus ignothus* larvae were observed to feed externally on second and third instars of *T. nigricornis*, which became yellowish, sluggish, and eventually died. The contents of the larvae were liquefied. The hymenopterous larvae were white with shades of gray and pink on their dorsa. Late instars of the parasitoid (0.4–0.8 mm wide; 0.9–2 mm long) were observed to change their diets. They fed and bored into a small portion of an achene, then pupated in the cavity so produced. They took 12–13 days ( $n = 3$ ) to emerge from their pupae (Table 1). Similarly, *Colotrechnus ignotus* was reported as a larval parasite of *T. actinobola* (Loew) (Stegmaier 1968). It was also reared from a *Tomoplagia cressoni* puparium (Goeden and Headrick 1991a).

The remaining parasitoid species recovered from *T. nigricornis* puparia were *Eurytoma* sp. and an unidentified perilampid. These were primary, solitary, larval-pupal endoparasitoids. They did not change the shape or behavior of the parasitized larvae, but they altered the size of the parasitized puparia, which became larger than unparasitized *T.*

*nigricornis* puparia: 1.4–1.5 mm in width and 3–3.3 mm in length for parasitized puparia ( $n = 7$ ) vs. 1–1.25 mm in width and 2.5–3 mm in length for healthy puparia ( $n = 100$ ). Also, both of these parasitoid species had a longer development period than other parasitoid spp.: 24–106 days for *Eurytoma* sp. and 56–111 days for the perilampid (Table 1).

*Eurytoma* species have been reported as parasitoids of other flower head-infesting tephritids. *Eurytoma vernonia* Bugbee was identified as a solitary, primary, larval-pupal endoparasitoid of *Neotephritis finalis* (Goeden et al. 1987), *Trupanea conjuncta* (Goeden 1987), *T. imperfecta* (Goeden 1988), and *Tomoplagia cressoni* (Goeden and Headrick 1991a). *Eurytoma* sp. was reared as parasitoids of *T. imperfecta* (Goeden 1988) and *Procecidochares lisae* (Silverman and Goeden 1980).

Percentage parasitism was much greater in samples infested with *T. nigricornis* than in samples infested with *T. bisetosa* (Table 2). Parasitism of *T. bisetosa* was 9.6% (range: 4.5–16.1) in *Helianthus annuus*, and only involved *Pteromalus* sp. On the other hand, parasitism was much higher, ranging from 21.5% to 58.2%, in host plants of *T. nigricornis*, and was caused by up to five species of parasitoids (Table 2). In the most common and widespread host of *T. nigricornis*, *Encelia farinosa*, total percentage parasitism was 30.4% (6.7–72.9%) and was caused by the five species identified above as *T. nigricornis* parasitoids, with *Halticoptera* sp. being the most abundant parasitoid species in those samples, followed closely by *Pteromalus* sp. (Table 3). In *E. frutescens*, total parasitism was 37.7% (13.8–51.5%) and involved the same five species of parasitoids with *Halticoptera* sp. and *Pteromalus* sp. again as the most numerous parasitoids (Table 3). Total percentage parasitism in *E. virginensis* was 37.9% (15.4–54.4%). It was caused by four species of parasit-

Table 2. Mean percentage total parasitism and comparison of parasitoids reared from flower heads samples from different host plants of *Trupanea nigricornis* and *T. bisetosa*.

Plant Species	Parasitism <sup>a</sup> (%) Mean ± SE (range)	N <sup>b</sup>	Reared Parasitoids <sup>c</sup>
<i>T. nigricornis</i> hosts:			
<i>Encelia farinosa</i>	30.4 ± 3.5 (6.7–72.9)	29	H, P, C, E, Pr
<i>E. frutescens</i>	37.7 ± 4.0 (13.8–51.5)	10	H, P, C, Pr, E
<i>E. virginensis</i>	37.9 ± 4.4 (15.4–54.4)	8	C, H, P, E
<i>Viguiera deltoidea</i>	21.5 ± 1.5 (20–23.1)	2	H, P
<i>Haploppapus venetus</i>	54.5 ± 3.6 (50.9–58.1)	2	P, E
<i>H. acradeniis</i>	58.2 ± 9.3 (47.1–76.8)	3	E, P, H
<i>T. bisetosa</i> hosts:			
<i>Helianthus annuus</i>	9.6 ± 0.6 (4.5–16.1)	18	P

<sup>a</sup> Parasitism was calculated by dividing the number of parasitoids confirmed as *T. nigricornis* or *T. bisetosa* parasitoids by the total number of dipterous insects and parasitoids that emerged from a host sample.

<sup>b</sup> Number of flower head samples.

<sup>c</sup> C = *Colotrechus ignothus*; E = *Eurytoma* sp.; H = *Halticoptera* sp.; P = *Pteromalus* sp.; Pr = perilampid. The parasitoids are listed in decreasing order of abundance.

toids, *C. ignothus*, being the most numerous, followed by *Halticoptera* sp., *Pteromalus* sp., and *Eurytoma* sp. (Table 3). Total parasitism in *Viguiera deltoidea* samples was 21.5% (20–23.1%) and only involved *Halticoptera* sp. and *Pteromalus* sp. (Table 3). In *Haploppapus venetus*, parasitism totaled 54.5% (50.9–58.1%) and was caused by *Pteromalus* sp. and *Eurytoma* sp. (Tables 2, 3). In *H. acradeniis* samples, total parasitism was the highest at 58.2% (47.1–76.8%) and was due to *Eurytoma* sp., which was the most numerous, followed by *Pteromalus* sp., and *Halticoptera* sp. (Table 3).

Out of a total of 54 samples belonging to different hosts of *T. nigricornis*, only three samples (5.6%) yielded *T. nigricornis* but no parasitoids (Table 4). Moreover, none of the 29 samples of *E. farinosa* collected during 4 years was free of parasitoids. *Encelia farinosa* is the most widespread host of *T. nigricornis* in southern California. On the other hand, 50% of the samples (20 out of 40) of *T. bisetosa* were free of parasitoids.

Some reasons that very few samples of *T. nigricornis* hosts were free of parasitoids may be: the hosts of *T. nigricornis* sampled are in bloom for only short

periods (ca. 2 months) in southern California; these hosts are usually heavily infested with *T. nigricornis*; *Trupanea nigricornis* populations have a high reproductive rate and make effective use of the plant resources available to them for only short periods; and these flies have an even distribution in the field. All these factors make *T. nigricornis* populations a reliable host for parasitoids.

In contrast, the greater number of *T. bisetosa* samples free parasitoids could be due to the following reasons: wild sunflower, the most common host of *T. bisetosa*, blooms throughout the year in southern California in the absence of frost; field populations of *T. bisetosa* larvae persist at low densities throughout the year as long as their hosts are present; the distribution of *T. bisetosa* in the field is uneven and clumped as flies are found only in a few patches within large populations of sunflowers; sunflower heads are covered with hard bracts and exude large amounts of resins when pierced, which probably deter most parasitoids from ovipositing in these heads.

The other common host plant of *T. bisetosa*, *Geraea canescens*, blooms only

Table 3. Total number of fly hosts and parasitoids reared from flower heads collected from all of the samples of the different hosts of *T. nigricornis* and *T. bisetosa*.

Flower Heads N <sup>a</sup>	Number and % of Reared Parasitoids <sup>b</sup>					Number and % of Reared Flies <sup>c</sup>					
	H	P	C	Pr	E	Tn	Nf	M	Tb	U	O
<i>T. nigricornis</i> hosts:											
<i>E. farinosa</i>											
13,860	517	241	46	2	8	1,379	934	55	—	—	1 <sup>d</sup>
	<b>63.5%</b>	29.6%	5.7%	0.2%	1%	<b>58.2%</b>	39.4%	2.3%	—	—	0.04%
<i>E. frutescens</i>											
2,690	59	40	9	2	1	165	12	43	—	—	—
	<b>53.2%</b>	36%	8.1%	1.8%	0.9%	<b>75%</b>	5.5%	19.5%	—	—	—
<i>E. virginensis</i>											
2,080	30	31	82	—	5	202	20	38	—	—	—
	20.3%	20.9%	<b>55.4%</b>	—	3.4%	<b>77.7%</b>	7.7%	14.6%	—	—	—
<i>H. acradenius</i>											
4,250	1	39	—	—	84	62	—	—	—	2	—
	0.8%	1.5%	—	—	<b>67.7%</b>	<b>96.9%</b>	—	—	—	3.1%	—
<i>H. venetus</i>											
1,980	—	41	—	—	4	34	—	—	—	3	2 <sup>e</sup>
	—	<b>91.1%</b>	—	—	8.9%	<b>87.2%</b>	—	—	—	7.7%	5.1%
<i>V. deltoidea</i>											
350	2	2	—	—	—	12	—	2	—	—	—
	<b>50%</b>	<b>50%</b>	—	—	—	<b>85.7%</b>	—	14.3%	—	—	—
<i>T. bisetosa</i> host:											
<i>H. annuus</i>											
3,660	—	107	—	—	—	—	272	18	685	—	12 <sup>f</sup>
	—	<b>100%</b>	—	—	—	—	27.6%	1.8%	<b>69.4%</b>	—	1.2%

<sup>a</sup> Total number of flower head collected from all samples.

<sup>b</sup> C = *Colotrechus ignothus*; E = *Eurytoma* sp.; H = *Halticoptera* sp.; P = *Pteromalus* sp.; Pr = perilampid.

<sup>c</sup> Tn = *Trupanea nigricornis*; Nf = *Neotephritis finalis*; M = *Melanagromyza viridis*; Tb = *T. bisetosa*; U = *Urophora formosa*; O = other tephritids;

<sup>d</sup> *T. wheeleri*;

<sup>e</sup> Nb = *Neaspilota brunneostigmata*;

<sup>f</sup> Pc = *Paracantha cultaris*.

In bold, are the dominant species of parasitoid and host fly per plant species.

Table 4. Host plant samples of *Trupanea nigricornis* and *T. bisetosa* that yielded flies but no parasitoids.

Plant Species	Number of Samples Free of Parasitoids	Total Number of Collected Flower Heads	Total Number of Reared Flies in Samples Free of Parasitoids <sup>a</sup>					
			Tn	Tb	Tw	Nf	M	Pc
Hosts of <i>T. nigricornis</i>								
<i>E. frutescens</i>	2	350	5	—	—	3	—	—
<i>H. acradenius</i>	1	500	1	—	1	—	—	—
Hosts of <i>T. bisetosa</i>								
<i>H. annuus</i>	18	2,250	—	105	6	—	15	1
<i>H. niveus</i>	1	110	—	2	—	—	3	—
<i>G. canescens</i>	3	745	—	21	—	—	152	—

<sup>a</sup> Tn = *Trupanea nigricornis*; Tb = *T. bisetosa*; Tw = *T. wheeleri*; Nf = *Neotephritis finalis*; M = *Melanagromyza viridis*; Pc = *Paracantha cultaris*.



Table 5. List of parasitoids and insects other than tephritids, agromyzids and their confirmed parasitoids that emerged from the samples of flower heads infested with *Trupanea nigricornis*.

Parasitoids and Insects Reared <sup>a</sup>	<i>Encelia farinosa</i> (4/29 sites) <sup>b</sup>	<i>Encelia frutescens</i> (2/10 sites)	<i>Encelia virginensis</i> (4/8 sites)	<i>Haplopappus acradenius</i> (3/3 sites)
<b>Parasitoids:</b>				
Braconidae	11	—	1	7
Cynipidae	—	—	1	—
Eucolilidae	2	5	2	—
Eulophidae	1 <sup>c</sup>	5 <sup>c, d</sup>	9 <sup>c, e, f</sup>	23 <sup>f</sup>
Eupelmidae	—	—	—	6
Platygasteridae	—	—	—	1
Pteromalidae	11 <sup>g</sup>	—	—	6 <sup>g</sup>
Torymidae	1	—	1 <sup>h</sup>	—
<b>Insect hosts:</b>				
Cecidomyiidae	+	+	+	+
Noctuidae	+	—	+	+
Curculionidae	—	—	—	+
Thrips	+	+	+	—

<sup>a</sup> Parasitoids not confirmed as tephritids' parasitoids and additional insects reared other than tephritids and agromyzids.

<sup>b</sup> Number of flower head samples (one sample per site) yielding these insects out of the total number of samples collected.

<sup>c</sup> *Eutetrastichus* sp. emerging from cecidomyiid galls.

<sup>d</sup> *Thripasoma grafi*.

<sup>e</sup> *Telenomus* sp.

<sup>f</sup> *Aprostocetus* sp.

<sup>g</sup> *Zatropus* sp.

<sup>h</sup> *Torymus* sp.

for a short period (1–2 months), like the various hosts of *T. nigricornis*, and its flower heads are not covered by hard bracts nor do they exude resins. The absence of parasitoids in the three samples of *G. canescens* that yielded *T. bisetosa* probably was because of the limited reproduction of this host plant for the four years of the study due to drought in southern California. The collected samples were heavily infested with generalist agromyzids and only a few *T. bisetosa*. The parasitoids probably were too scarce and less efficient at detecting this plant.

Other parasitoids were recovered from flower heads of *T. nigricornis* and *T. bisetosa* host plants, but they were not reared from individual larvae or puparia of *T. nigricornis* and *T. bisetosa* and thus were not confirmed as parasitoids of these tephritids. The parasitoids and insects, other than dipterous flies, that

emerged from some of the host samples also containing *T. nigricornis* are listed in Table 5. The Hymenoptera include braconids, torymids, platygasterids, cynipids, eupelmids, *Zatropus* sp. (Pteromalidae), and eulophids. The eulophids consisted of several genera: *Telenomus* sp., a parasitoid of lepidopterous eggs, *Eutetrastichus* sp., *Thripasoma grafi* Crawford, four species of *Aprostocetus* sp., and an identified species of eulophid that emerged from cecidomyiid galls. Other non-dipterous insects that occurred in these samples were noctuids, curculionids, free-living, predacious cecidomyiids, gall-forming cecidomyiids, anthocorids, aphids, and thrips. The parasitoids and non-dipterous insects that emerged from samples of hosts also containing *T. bisetosa*, i.e., *Helianthus annuus* and *H. niveus*, included braconids, eulophids, noctuids, aphids, and anthocorids.



It was not determined whether the eulophids, braconids, torymids and the other reared parasitoids also parasitized *T. nigricornis* or *T. bisetosa* because they were not individually reared from these tephritids and some may have been hyperparasitic.

In addition to parasitism, adults of *T. nigricornis* and *T. bisetosa* suffered mortality in the field due to predation. Both jumping spiders (Salticidae) and crab spiders (Thomisidae) commonly attacked adults of *T. nigricornis* and *T. bisetosa*. The spiders were observed hiding under leaves and bracts of flower heads and they ambushed newly emerged adult males ( $n = 5$ ) during resting ( $n = 5$ ) or courtship ( $n = 3$ ) and females during probing or oviposition ( $n = 10$ ). They were not specific to *Trupanea* spp. as they also were observed to capture *Neotephritis finalis* females ( $n = 4$ ) while they were probing on wild sunflower heads. Coccinellid larvae were observed ( $n = 4$ ) to prey on newly emerged *T. nigricornis* adults on *E. farinosa* flower heads in the field and in insectary cages. Noctuid larvae feeding within *E. farinosa* flower heads occasionally killed any *T. nigricornis* larvae they encountered.

Spiders and birds have been reported as potential mortality factors of other flower head-infesting tephritids. Jumping and crab spiders were common predators of *Trupanea conjuncta* adults (Goeden 1987) and *Paracantha gentilis* adults (Headrick and Goeden 1990). The jumping spider, *Pellenes signatus* (Banks), was observed preying on adults of *Procecidochares lisae* (Silverman and Goeden 1980). Spiders were also reported to prey on adults of the gall-forming species of the genus *Valentibula* (Wangberg 1978). The inquiline *Mordellistena unicolor* LeConte (Coleoptera: Mordellidae) was reported to attack galls of *Eurosta solidaginis* (Fitch) of different diameters; moreover, avian birds, such as, downy woodpeckers and black-capped chicka-

dees, were commonly observed to break large galls and prey on these larvae during the winter months (Abrahamson et al. 1989). Heavy predation by birds was also observed on the overwintering larvae of the gall-forming species *Tephritis baccharis* (Goeden and Headrick 1991b) and *Eutreta diana* (Osten Sacken) (Goeden 1990). Moreover, *E. diana* larvae were subject to predation by unidentified clerid larvae and to occasional killing by Lepidoptera and Coleoptera (*Apion* sp., Apionidae) larvae that were feeding as inquilines inside the galls (Goeden 1990). In the gall-forming *Procecidochares* spp., the inquiline curculionid, *Apion* sp., occasionally killed the resident tephritid larvae, and beetle larvae of *Phyllobaenus* sp. (Cleridae) were general predators of the gall-former (Wangberg 1980). In *Chaetostomella undosa* (Coquillett), ants were reported to prey on the pupae and centipedes occasionally preyed on larvae (Steck 1984).

In summary, both parasitoids and predators imposed important mortality factors on the immatures and adults of *T. nigricornis* and *T. bisetosa*. The parasitoids attacking these species were generalists that attacked larvae of other dipterous larvae. The impact of natural enemies on these two closely related species that have adopted different modes of herbivory was significantly different. By adopting a narrowly oligophagous mode of herbivory and mainly specializing on wild sunflowers in southern California, *T. bisetosa* is restricting its diet breadth, but appears to escape from natural enemies. *Trupanea bisetosa* was attacked by fewer parasitoid species (one vs. five identified species) and had much lower total parasitism rates than the generalist *T. nigricornis*. Although these two sympatric species do share one host plant genus, *Geraea* (Goeden 1992), that could represent the ancestral host genus of both species or

just another expansion to the host range of either tephritids, the exact causes that lead to the speciation of these two species cannot be known. However, natural enemies constitute one of the reasons causing diet specialization. Lack of 'enemy-free' space for phytophagous insects can be the critical factor limiting new species from colonizing a certain plant (Strong et al. 1984). Further, "host-plant use or changes in use that reduce predation are advantageous... Within a given place and time, preference for a plant less likely to be visited by natural enemies could evolve rapidly. Specializations for continued avoidance of predators may also then be rapidly selected for and established" (Bernays and Graham 1988). Thus, natural enemies may constitute an important factor that limits insect host range (Bernays and Graham 1988). Additionally, the biophysical features of plants are important factors in determining host suitability (Zwölfer and Harris 1971). Biophysical features of wild sunflowers, such as resins and toughness of the bracts, might then limit the number of parasitoid species able to attack *T. bisetosa*, by making it difficult for the parasitoids to gain access to *T. bisetosa* larvae in the flower heads.

In other tephritids, host shifts have been recorded that resulted in escape from natural enemies (Feder 1995). Experiments demonstrated that parasitoid attack was much lower in the derived apple race of *Rhagoletis pomonella* (Walsh) than in the ancestral hawthorn race. The bigger apple host was found to provide a physical refuge for the apple maggot larvae from the parasitoids. Therefore, enemy-free space was one important factor in host range expansion and host formation in *R. pomonella* (Feder 1995). It appears that the "major processes acting in many communities work vertically through the food chain, not horizontally with other species in the

same trophic level" (Strong et al. 1984). Thus, by specializing on a few host plants, *T. bisetosa* gained some protection from potential natural enemies.

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